

REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF  
CENTRAL WYOMING. PART 12. NEW SPECIES OF OMOMYID  
PRIMATES (MAMMALIA: PRIMATES: OMOMYIDAE) AND  
OMOMYID TAXONOMIC COMPOSITION ACROSS THE  
EARLY-MIDDLE EOCENE BOUNDARY

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ABSTRACT

Ongoing paleontological field work has resulted in the recovery of fossils representing four new species of omomyid primates from the Lost Cabin Member of the Wind River Formation, northeastern Wind River Basin, central Wyoming. *Hemiacodon casamissus*, n. sp., is the oldest (latest Wasatchian or Lostcabinian) known species of *Hemiacodon*, a genus otherwise restricted to the late Bridgerian (Twinbuttean). The dental anatomy of *H. casamissus* suggests that *Hemiacodon* is an aberrantly specialized washakiin genus which shares most recent common ancestry with a clade consisting of *Washakius* and *Dyseolemur*. *Trogolemur amplior*, n. sp., and the lithosympatric *T. fragilis*, n. sp., are the oldest (earliest Bridgerian or Gardnerbuttean) known species of this highly specialized anaptomorphine genus. The upper and lower molar morphology of *Trogolemur* suggests that the closest relatives of this genus are *Tetonoides*, *Arapahovius* and *Anemorhysis*. The content of the previously monotypic tribe Trogolemurini is therefore expanded to include the latter three genera. *Anemorhysis natronensis*, n. sp., is the youngest known (Gardnerbuttean) species of *Anemorhysis*. It likely shares most recent common ancestry with *A. pattersoni*. The phylogeny of *Anemorhysis* is complex; at least two lineages of *Anemorhysis* appear to have coexisted throughout most of its stratigraphic range.

An important restructuring in the taxonomic composition of the North American omomyid primate fauna occurred around the Wasatchian-Bridgerian boundary. At that time, global climatic warming may have contributed to a gradual turnover in omomyid taxonomic composition at the subfamilial level, with Omomyinae replacing Anaptomorphinae as the dominant component of omomyid faunas. This restructuring had an important consequence for the later evolution of Omomyidae in North America, as omomyines continued to diversify while only one anaptomorphine, the extremely rare and dentally specialized *Trogolemur*, is known to have survived beyond Bridgerian time.

INTRODUCTION

Many seasons of collecting the mammalian fauna of the upper part of the Wind River Formation in the Wind River Basin of central Wyoming have resulted in the recovery of fossils representing four new species of omomyid primates. The upper part of the Wind River Formation traverses the Wasatchian-Bridgerian (early-middle Eocene) boundary (Stucky, 1984a, 1984b, 1984c; Krishtalka et al., 1987), and thus yields mammalian fossils intermediate in age between the "classic" early and middle Eocene faunas known from the Willwood and Bridger formations of northwestern and southwestern Wyoming, respectively (e.g., Cope,

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1881; Stucky, 1984c; Krishtalka et al., 1987). The early and middle Eocene omomyid faunas from those formations share no genera in common, reflecting a marked change in omomyid taxonomic composition between the times of deposition of those rock units. Thus, the omomyids of the upper part of the Wind River Formation provide critical insight into this taxonomic reorganization, which was arguably the most important event influencing the later evolution of omomyids in North America.

In this report we formally describe four new species of omomyids from the upper part of the Wind River Formation and assess their significance for understanding the phylogeny of North American Omomyidae. We also present a climatic hypothesis that may account for the taxonomic reorganization of the omomyid primate fauna across the Wasatchian-Bridgerian boundary.

Institutional abbreviations used in this report are as follows: ACM, Pratt Museum of Geology, Amherst College (Amherst, Massachusetts); AMNH, American Museum of Natural History (New York, New York); CM, Carnegie Museum of Natural History (Pittsburgh, Pennsylvania); UALP, University of Arizona Laboratory of Paleontology (Tucson, Arizona); UCM, University of Colorado Museum (Boulder, Colorado); USGS, Paleontology-Stratigraphy Branch, U.S. Geological Survey (Denver, Colorado); YPM-PU, Princeton University paleontological collections now housed at Yale Peabody Museum (New Haven, Connecticut).

#### SYSTEMATIC PALEONTOLOGY

Order Primates Linnaeus, 1758

Suborder Haplorhini Pocock, 1918

Infraorder Tarsiiformes Gregory, 1915

Family Omomyidae Trouessart, 1879

Subfamily Anaptomorphinae Cope, 1883

Tribe Trogolemurini Szalay, 1976

*Type genus.*—*Trogolemur* Matthew, 1909.

*Included genera.*—*Trogolemur* Matthew, 1909; *Anemorhysis* Gazin, 1958; *Tetonoides* Gazin, 1962; *Arapahovius* Savage and Waters, 1978.

*Emended diagnosis.*—Anaptomorphines with relatively large  $M_3$  and  $M^3$ .  $P_4$  with buccolingually wide talonid and cristid obliqua joining trigonid buccally. Molar talonids deeply basined, with weakly inflated talonid cusps peripheral in position.  $M_1$  relatively longer and narrower than in Anaptomorphini.  $M_{2-3}$  with protoconid and metaconid cusps widely separated, paraconid lingual in position, and with shelf-like paracristid resulting in relatively well-developed mesial trigonid fovea. Upper molars (unknown in *Anemorhysis*) with enhanced development of postprotocingulum.  $M^3$  with well-developed postprotocrista continuous with lingual crest from metacone near metaconule.

*Discussion.*—Szalay (1976) divided the subfamily Anaptomorphinae into the tribes Anaptomorphini and Trogolemurini, the latter including only *Trogolemur myodes*. Thus, the tribe Trogolemurini was originally proposed solely on the basis of the phenetic distinctiveness of *T. myodes* with respect to other anaptomorphines, a point made explicitly by Szalay (1976:255).

The two new species of *Trogolemur* described below (particularly *T. amplior*) provide insight into the phylogenetic position of *Trogolemur*, because they possess what we interpret as a more primitive molar morphology than that of *T. myodes*. In light of these new species and reassessment of other anaptomorphine specimens,

a number of dental synapomorphies appear to define a clade of anaptomorphines consisting of the genera *Tetonoides*, *Anemorhysis*, *Arapahovius* and *Trogolemur*. Using *Teilhardina belgica* and *Steinius vespertinus* as approximations of the omomyid dental morphotype (Rose and Bown, 1991), derived dental traits shared by *Tetonoides*, *Anemorhysis*, *Arapahovius* and *Trogolemur* include most of the features listed above in the tribal diagnosis. Exceptions include the relatively large upper and lower third molars, the relatively long and narrow  $M_1$ , and the deeply basined lower molar talonids bearing weakly inflated, peripherally situated talonid cusps that are found in both Trogolemurini and the primitive omomyine *S. vespertinus* (Bown and Rose, 1984; Rose and Bown, 1991). We hypothesize that the dental characters shared by Trogolemurini and *S. vespertinus* are sympleiomorphies, and that the alternative character states found in Anaptomorphini are derived.

Given these considerations, we have modified Szalay's (1976) concept of the Trogolemurini, making it a more inclusive grouping than originally proposed. Such a taxonomic change is required in order to maintain the Anaptomorphini (*sensu* Szalay, 1976; i.e., including *Anemorhysis*) as monophyletic. Although the monophyly of the Trogolemurini as defined here can be defended on dental evidence, interrelationships among the included genera are not yet clear.

The postcranial anatomy of members of the Trogolemurini remains poorly known, as is the case for omomyids in general. Only a few isolated tarsal elements and a distal tibia have been referred to *Arapahovius gazini* (Savage and Waters, 1978; Gebo, 1988), the only trogolemurinin for which postcranial elements have been identified. Given our meager knowledge of the postcranium in Anaptomorphinae, it is interesting that the tarsals of *Arapahovius gazini* differ from those of the anaptomorphinins *Teilhardina belgica* and *Tetonius homunculus* in ways that suggest a greater emphasis on leaping in *A. gazini* (Savage and Waters, 1978; Gebo, 1988). Hence, it is possible that postcranial features will also prove to be diagnostically different in Trogolemurini and Anaptomorphini, once better representation of the postcranium in Anaptomorphinae is acquired.

#### *Anemorhysis* Gazin, 1958

*Type species.*—*Paratetonius? sublettensis* Gazin, 1952.

*Included species.*—*Anemorhysis sublettensis* (Gazin, 1952); *A. wortmani* Bown and Rose, 1984; *A. pattersoni* Bown and Rose, 1984; *A. natronensis*, n. sp.

#### *Anemorhysis natronensis*, new species

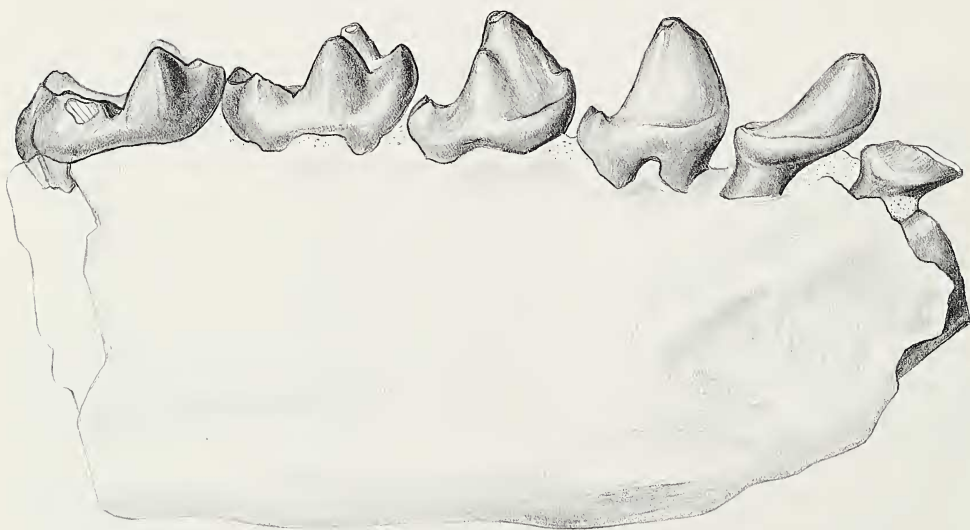
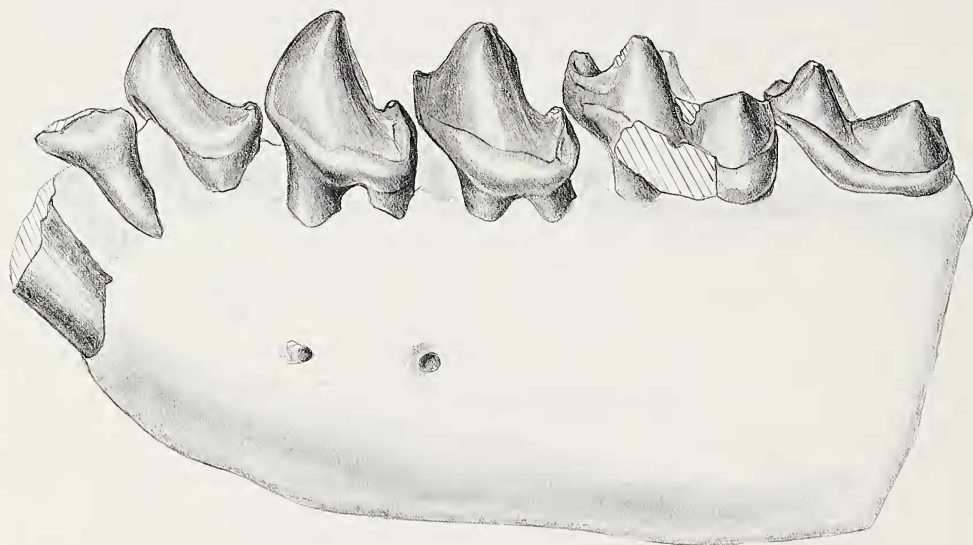
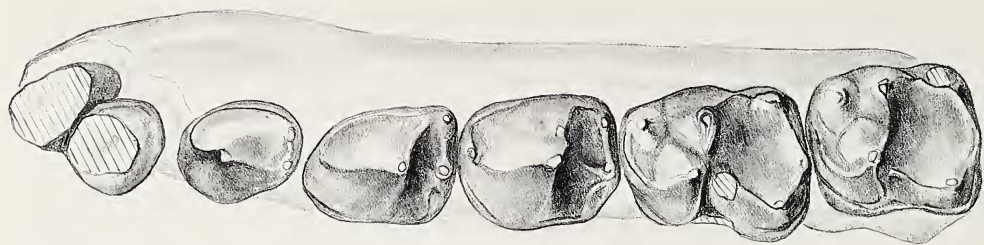
(Fig. 1)

*Holotype.*—CM 41137 (Fig. 1), left dentary fragment preserving root of  $I_1$ , crowns of  $I_2$  (broken),  $C_1$ ,  $P_{3-4}$ ,  $M_{1-2}$ ; only known specimen.

*Type locality.*—CM loc. 34, Natrona County, Wyoming.

*Known distribution.*—*Eotitanops* (= *Palaeosyops*) *borealis* Assemblage Zone (Gardnerbuttean, earliest Bridgerian), Lost Cabin Member, Wind River Formation, Wind River Basin, Wyoming (for definitions and discussion of Eocene biostratigraphic units used in this paper see Stucky, 1984a; Krishtalka et al., 1987; Stucky et al., 1990).

*Diagnosis.*—Paraconid of  $P_4$  weakly developed, inferior in position, and widely separated from metaconid, in contrast to *A. wortmani* and *A. sublettensis*.  $P_4$  longer, less exodaenodont, and with slightly better developed paraconid than in *A. pattersoni*. Dentary more shallow than that of *A. pattersoni*, with less mesiodistal



compression of  $I_2$ – $P_3$  and with less hypertrophy of  $I_1$  (judging from roots or alveoli for these teeth in *A. pattersoni*). Paraconid of  $M_2$  less connate with metaconid than in *A. pattersoni*.

*Etymology.*—Named for Natrona County, Wyoming.

*Description.*—The anterior dentition is more complete in CM 41137 than in any other specimen of *Anemorhysis*, yielding a lower dental formula of 2-1-2-3 for *A. natronensis*.

The crowns of the incisors of *A. natronensis* (CM 41137) are missing. From the preserved root of  $I_1$  and the broken crown of  $I_2$ , it is apparent that  $I_1$  was larger than  $I_2$ , although the difference in size appears not to have been great. The relatively minor hypertrophy of  $I_1$  found in *A. natronensis* compared to other species of the genus (particularly *A. pattersoni* and *A. wortmani*) is apparently correlated with its comparatively shallow dentary (depth of the dentary below  $M_1$  in CM 41137 is 3.1 mm, whereas the same measurement in USGS 476, holotype of *A. pattersoni*, is 4.4 mm; see Beard, 1987).

The lower canine measures 1.20 mm (mesiodistal length, L)  $\times$  0.95 mm (buccolingual width, W). The crown is canted strongly mesially and is simple in morphology, being dominated by the protoconid. A weak lingual cingulid runs continuously from the lingual aspect of the apex of the protoconid to the diminutive talonid heel of the tooth, where it joins a tiny cuspule that may represent a weak entoconid. A similarly weak cuspule is developed in the hypoconid region of the talonid heel. There is no ectocingulid.

$P_3$  measures 1.40 mm (L)  $\times$  1.15 mm (W) and is double-rooted. The trigonid bears only the protoconid. There is a weak lingual cingulid as in  $C_1$ , but this structure is not continuous in  $P_3$ , being interrupted near the lingual side of the postvallid. A weak crest runs inferiorly from the apex of the protoconid toward the entoconid, but it does not join that cusp. The extremely short and shallowly basined talonid bears both an entoconid and a hypoconid, with the latter cusp being more prominent. There is no appreciable development of a cristid obliqua on  $P_3$ .

$P_4$  measures 1.50 mm (L)  $\times$  1.30 mm (W). The tooth is morphologically very similar to  $P_3$ , from which it differs in being somewhat more molariform. The trigonid bears both a paraconid and metaconid in addition to the protoconid. The paraconid is situated very inferiorly on the crown and is weakly developed with respect to the metaconid. The latter two cusps are widely separated mesiodistally, in contrast to the condition in *A. wortmani* and *A. sublettensis*. A weak lingual cingulid is present between the paraconid and metaconid. The talonid is mesiodistally longer and more clearly basined on  $P_4$  than  $P_3$ , and it possesses both a hypoconid and an entoconid as in the latter tooth. A weak cristid obliqua unites the hypoconid with the postvallid.

$M_1$  measures 1.80 mm (L)  $\times$  1.40 mm (W). The crown is morphologically typical of the genus *Anemorhysis* and is very similar to that of *A. pattersoni* (Bown and Rose, 1984). It differs from  $M_1$  in *A. wortmani* in that the cristid obliqua does not join the metaconid.

$M_2$  measures 1.80 mm (L)  $\times$  1.30 mm (W). Like  $M_1$ , the crown of  $M_2$  is morphologically similar to those of other species of *Anemorhysis*. It differs slightly from the  $M_2$  of *A. pattersoni* in having the paraconid and metaconid less connate.

*Discussion.*—*Anemorhysis natronensis*, from the earliest part of the Bridgerian Land Mammal Age, is the youngest known species of the genus. Despite its young age, in certain respects *A. natronensis* is more primitive than any of the older species of the genus currently known. These features of *A. natronensis* would appear to reflect the complicated pattern of phylogeny of *Anemorhysis*, a genus which, in terms of numerical abundance, remains one of the most poorly represented anaptomorphines (Bown and Rose, 1984, 1987).

The anterior dentition is more completely preserved in *A. natronensis* than in any other species of the genus. Thus, a lower dental formula of 2-1-2-3 is well established for this species. A similar lower dental formula may also characterize *A. pattersoni* and *A. wortmani* (Bown and Rose, 1984). However, Bown and Rose (1987:43) later suggested that "The probable absence of  $p_2$  in the holotype of *A.*

←  
Fig. 1.—*Anemorhysis natronensis*, n. sp., holotype, CM 41137. Left dentary fragment preserving root of  $I_1$ , crowns of  $I_2$  (broken),  $C_1$ ,  $P_{3-4}$ ,  $M_{1-2}$ . Top to bottom: occlusal, buccal and lingual views. Scale equals 5 mm.

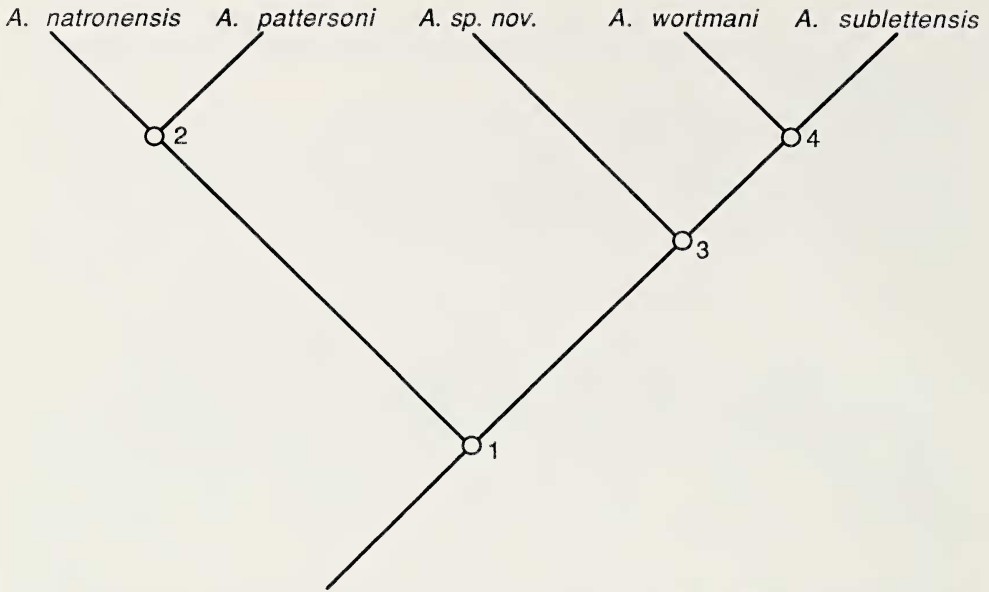


Fig. 2.—Cladogram depicting species-level relationships within the genus *Anemorhysis*. See text for discussion of synapomorphies supporting each node.

*pattersoni* . . . , upon restudy, seems equivocal. It is just as likely that the two small compressed alveoli anterior to the two roots of p3 contained c and p2, and that damage at the back of the i1 alveolus has obliterated a diminutive i2 alveolus." Despite these appropriately cautious observations, the dental formula of *A. natronensis* supports the earlier interpretation of Bown and Rose (1984), who favored a more reduced dental formula for *A. pattersoni*. *Anemorhysis natronensis* closely resembles *A. pattersoni* in most aspects of its morphology. Indeed, the most significant morphological differences between *A. natronensis* and *A. pattersoni* are the increased mesiodistal compression of I<sub>2</sub>-P<sub>3</sub>, greater hypertrophy of I<sub>1</sub>, and deeper dentary in *A. pattersoni*. For these reasons, it is difficult to imagine that *A. pattersoni* retained a premolar (P<sub>2</sub>) that was lost in *A. natronensis*, while at the same time evolving a more foreshortened dentary with a more hypertrophied I<sub>1</sub> than occurs in that species. Thus, it seems probable that the lower dental formula for *A. pattersoni* is the same as that for *A. natronensis* (2-1-2-3), although more complete specimens of the former species are required to verify such an hypothesis.

As the genus is defined in this paper, the monophyly of *Anemorhysis* can be defended on the basis of the following three synapomorphies (using the closely related taxa *Tetonoides pearcei* and *Arapahovius gazini* as outgroups): (1) I<sub>1</sub> larger than I<sub>2</sub>; (2) some degree of foreshortening of dentary; (3) talonid of P<sub>4</sub> variably basined and buccolingually wide, with entoconid and hypoconid widely separated (Fig. 2, node 1). The species *Tetonoides pearcei*, originally proposed by Gazin (1962) and often classified as a species of *Anemorhysis* (e.g., Bown, 1974; Szalay, 1976; Bown and Rose, 1984, 1987), is excluded from *Anemorhysis* here because it lacks these synapomorphies. Such a view has also been endorsed by Savage and Waters (1978), Bown (1979a), and Gingerich (1981). We agree with Savage and Waters (1978:16) that *Tetonoides pearcei* may share more recent common ancestry with *Arapahovius* (and/or *Trogolemur*) than with *Anemorhysis*, although the sim-

ilarities shared by *Tetonoides* and *Arapahovius* may also be trogolemurinin symplesiomorphies, indicative of no closer relationship than their common tribal affiliation. In either case, *Tetonoides pearcei* is best kept distinct from either *Anemorhysis* or *Arapahovius*, at least until its phylogenetic relationships are better understood.

The known species of *Anemorhysis* appears to comprise two clades, each containing two or more species. These two clades are most easily distinguished on the basis of their lower premolars. One of these clades, that comprising *A. pattersoni* and *A. natronensis* (Fig. 2, node 2), is characterized by the derived loss of one lower premolar ( $P_2$ ) coupled with generally primitive lower premolar morphology. In *A. pattersoni* and *A. natronensis*, the paraconid and metaconid on  $P_4$  are widely separated and the paraconid is weakly developed and inferior in position compared to the condition in *A. wortmani* and *A. sublettensis* (Bown and Rose, 1984, 1987).  $P_3$  in *A. natronensis* also differs considerably from this tooth in *A. wortmani* in having a much longer trigonid and in being double-rooted. The crown of  $P_3$  is unknown in both *A. pattersoni* and *A. sublettensis*, but this tooth is double-rooted in *A. pattersoni*, as in *A. natronensis* but in contrast to *A. wortmani* (Bown and Rose, 1984, 1987). In all of these aspects of lower premolar morphology, *A. pattersoni* and *A. natronensis* resemble the condition in very primitive anaptomorphines such as *Teilhardina belgica* and *T. americana* (Bown and Rose, 1987). For this reason, the premolar morphology of these two species (especially that of *A. natronensis*) likely approximates the primitive condition for the genus.

A more derived lower premolar morphology occurs in *A. wortmani*, *A. sublettensis* and an undescribed species of *Anemorhysis* from Lysitean rocks in the Washakie Basin of southern Wyoming (H. H. Covert, 1990, personal communication) that we believe to be the sister taxon of a clade including *A. wortmani* and *A. sublettensis* (Fig. 2, node 3). In all of these species the trigonids of  $P_{3-4}$  are derived in being mesiodistally compressed compared to the condition in *A. pattersoni* and *A. natronensis*. The lower fourth premolar is further derived in the clade including *A. wortmani* and *A. sublettensis* (Fig. 2, node 4) in that the paraconid of  $P_4$  is strongly cuspidate, closely appressed to the metaconid, and joined to the protoconid by a well-developed, strongly arcuate paracristid. Two additional derived features occur in the premolars mesial to  $P_4$  in *A. wortmani*, but the relevant anatomy remains unknown in *A. sublettensis*. As is the case in the clade including *A. pattersoni* and *A. natronensis*,  $P_2$  is lost in *A. wortmani* (Bown and Rose, 1984, 1987). However, the loss of  $P_2$  clearly occurred in parallel in *A. wortmani* on the one hand and in the *A. pattersoni* + *A. natronensis* clade on the other, because this tooth is retained in the undescribed species of *Anemorhysis* from the Washakie Basin (H. H. Covert, 1990, personal communication).  $P_3$  in *A. wortmani* is derived compared to that in all other species of *Anemorhysis* for which the relevant anatomy is known ( $P_3$  remains unknown only in *A. sublettensis*) in being single-rooted (Bown and Rose, 1984, 1987). More nearly complete fossils of *A. sublettensis* are required to resolve whether the loss of  $P_2$  and the presence of a single-rooted  $P_3$  in *A. wortmani* are autapomorphies for that species or else form additional synapomorphies for the *A. wortmani* + *A. sublettensis* clade. A similar conclusion concerning the sister group relationship between *A. wortmani* and *A. sublettensis* was reached by Bown and Rose (1984, 1987).

The known stratigraphic occurrences of the four species of *Anemorhysis* demonstrate that throughout much, if not all, of its temporal duration the genus was composed of two contemporaneous clades.

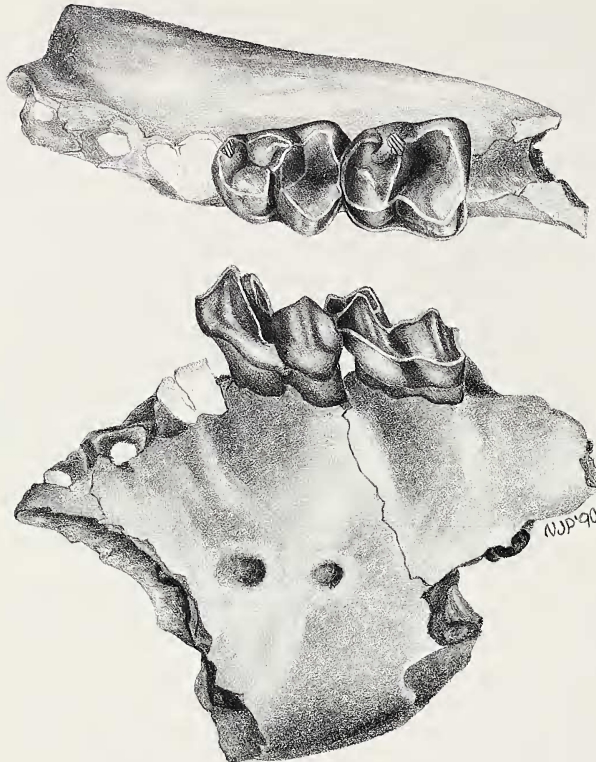


Fig. 3.—*Trogolemur amplior*, n. sp., holotype, CM 40069. Left dentary fragment preserving crowns of  $M_{1-2}$ , roots or alveoli for  $I_1$ ,  $C_1$ ,  $P_{3-4}$ . Views are occlusal (top) and buccal (bottom). Scale equals 10 mm.

*Trogolemur* Matthew, 1909

*Trogolemur amplior*, new species

(Fig. 3, 4)

*Holotype*.—CM 40069 (Fig. 3), left dentary fragment preserving crowns of  $M_{1-2}$ , roots or alveoli for  $I_1$ ,  $C_1$ ,  $P_{3-4}$ .

*Hypodigm*.—The holotype and possibly UCM 46602, isolated left  $P_3$  (Fig. 4).

*Type locality*.—CM loc. 34, Natrona County, Wyoming.

*Known distribution*.—*Eotitanops borealis* Assemblage Zone (Gardnerbuttean, earliest Bridgerian), and possibly (if UCM 46602 is correctly referred) *Lambdotherium* Range Zone (UCM loc. 80062, Lostcabinian, latest Wasatchian), Lost Cabin Member, Wind River Formation, Wind River Basin, Wyoming.

*Diagnosis*.—Larger than *T. myodes*, with deeper dentary. Talonids of  $M_{1-2}$  more deeply basined and wider in relation to trigonids than in *T. myodes*.

*Etymology*.—Latin *amplior*, larger; with reference to the comparatively large size of the species.

*Description*.—The holotype of *T. amplior*, CM 40069, preserves roots or alveoli for most if not all of the dentition mesial to the crown of  $M_1$ . The most mesial and the largest of these alveoli harbors



the broken root of  $I_1$ , which extends distally at least as far as the talonid of  $M_2$ . Thus, the unknown  $I_1$  crown of *T. amplior* was evidently enlarged and procumbent, and its root extended beneath the lower molars, as occurs only in *Trogolemur* among known omomyids.

Between the alveolus for  $I_1$  and the crown of  $M_1$  in CM 40069, there are three alveoli. These increase in circumference distally, thus having the same relative proportions as the alveoli for the teeth interpreted as  $C_1$ ,  $P_3$ , and  $P_4$  in *T. myodes* (Gazin, 1958; Szalay, 1976). By analogy with *T. myodes*, these three alveoli are also interpreted as having supported single-rooted  $C_1$ ,  $P_3$ , and  $P_4$  in CM 40069. If so, the relative proportions of the crowns of these teeth in *T. amplior* are likely to have been the same as those in *T. myodes*. There is no evidence of a diminutive, laterally placed alveolus for  $I_2$  in CM 40069, contrary to the condition in the holotype of *T. myodes* (AMNH 12599; see Gazin, 1958; Szalay, 1976). However, breakage may have obscured this structure in CM 40069.

$P_3$ , preserved in the tentatively referred specimen UCM 46602 (see below), measures 1.20 mm (L)  $\times$  0.95 mm (W). The protoconid is low and canted mesially. Mesial and distobuccal crests run inferiorly from the apex of the protoconid. Neither paraconid nor metaconid is present. A mesiodistally short but transversely wide talonid heel bears tiny cuspules that may represent incipient hypoconid and entoconid cusps. The crown bears labial and lingual cingulids and is noticeably exodaenodont.

$M_1$  measures 2.20 mm (L)  $\times$  1.85 mm (W). The trigonid bears the normal three cusps, although the apex of the paraconid is broken. Apparently, the latter was situated farther buccally and mesially than is the case on  $M_2$ . A similar condition exists in *T. myodes*. The protoconid is slightly taller than the metaconid and is separated from it by a prominent valley that arcs mesiolingually, where it separates the metaconid from the broken paraconid, thus resulting in a lingually open trigonid. A well-developed paracristid unites the apex of the protoconid with the broken paraconid. The talonid is appreciably wider than the trigonid, is deeply basined, and is surrounded on all sides by well-developed crests, all of which are in contrast to the condition in *T. myodes*. The cristid obliqua runs in arcuate fashion from the hypoconid to the metaconid, thus resulting in a relatively deep hypoflexid. A partial postcingulid runs between the hypoconid and the poorly-developed hypoconulid. The ectocingulid is only faintly developed, being best expressed on the buccal surface of the protoconid. Two small lobes of enamel extend inferiorly on the buccal surfaces of the protoconid and hypoconid cusps, making the  $M_1$  crown as a whole slightly exodaenodont.

$M_2$  measures 1.95 mm (L)  $\times$  1.95 mm (W). In contrast to the condition in  $M_1$ , the paraconid is fully lingual in position and connate with the metaconid, the paracristid is shelf-like rather than crestiform, the talonid and trigonid are more nearly equal in width, and the cristid obliqua terminates farther buccally on the postvallid rather than joining the metaconid. The ectocingulid is more nearly complete on  $M_2$  than  $M_1$ , extending continuously from the protoconid to the distal aspect of the hypoconid where it joins a partial postcingulid. Overall, the features that differentiate  $M_1$  from  $M_2$  in *T. amplior* also occur in *T. myodes*.

The dentary of *T. amplior* is extremely deep to accommodate the hypertrophied  $I_1$ , being even more specialized in this regard than *T. myodes*. Beneath the talonid of  $M_1$  in CM 40069, the dentary measures 5.80 mm in depth (measured lingually). The same measurement in a specimen of *T. myodes* (CM 13921) is 3.90 mm.

*Discussion.*—UCM 46602 (Fig. 4), an isolated left lower premolar tentatively referred to *Trogolemur amplior*, was previously identified as a possible  $P_2$  of an indeterminate omomyid, having been compared with that tooth in *Chlororhysis knightensis* (Stucky, 1982). However, UCM 46602 differs considerably from  $P_2$  in *C. knightensis* and other omomyids that we have examined (*Shoshonius*, *Tetoni*, *Absarokius*, *Arapahovius*, *Teilhardina*) in having a strongly developed distobuccal crest running from the protoconid to the talonid heel and in having a relatively well-developed talonid with diminutive cuspules in the hypoconid and entoconid positions. In these respects, the tooth compares much more closely with the single-rooted  $P_3$  in *Trogolemur myodes* and *Anemorhysis wortmani* (Gazin, 1958; Szalay, 1976; Bown and Rose, 1984). Further evidence that UCM 46602 represents a single-rooted  $P_3$  rather than a  $P_2$  comes from the root of the tooth, which is strongly compressed mesiodistally, suggesting that the anterior dentition and the dentary as a whole were greatly foreshortened. Crowding of the antemolar teeth related to anterior foreshortening of the lower jaw could have led to the coalescence of the two roots normally found in omomyid  $P_3$ s, as apparently occurred in the anagenetic transformation from *Tetoni* *matthewi* to *Pseudote-*

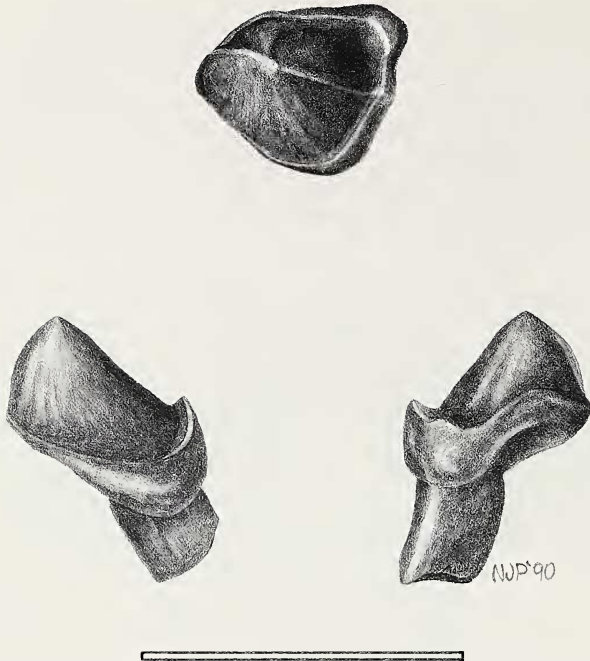


Fig. 4.—*Trogolemur amplior*, n. sp., UCM 46602. Isolated left  $P_3$ . Views are occlusal (top), buccal (bottom left) and lingual (bottom right). Scale equals 2 mm.

*tonius ambiguus* (Bown and Rose, 1987). UCM 46602 resembles the  $P_3$  of *T. myodes* more than that of *A. wortmani* in having a lower, more mesially canted protoconid.

*Trogolemur amplior* is the largest known species of *Trogolemur*, and its molar morphology seems more primitive than that of *T. myodes*. In particular, the more deeply basined talonids of the lower molars of *T. amplior* approximate the condition found in earlier and more primitive trogolemurinins such as *Tetonoides*, *Anemorhysis*, and *Arapahovius* (Savage and Waters, 1978; Bown and Rose, 1984, 1987, 1991). *Trogolemur amplior* further resembles these genera in possessing weakly inflated molar talonid cusps that are peripheral in position, a cristid obliqua on  $M_1$  that joins the metaconid, and a fully lingual paraconid and shelf-like paracristid that result in a relatively well-developed mesial trigonid fovea on  $M_2$ . Although  $M_3$  is unknown in *T. amplior*, that of *T. myodes* bears an additional similarity to those of *Tetonoides* and *Arapahovius* in that it is larger than is typical for anaptomorphinins. We view the common lower molar morphology of *T. amplior*, *Tetonoides*, *Arapahovius*, and *Anemorhysis* as morphotypic for the tribe Trogolemurini, while the different lower molar morphology characteristic of *T. myodes* appears to be autapomorphic for that species.

Some workers have entertained the possibility of a close relationship between *Trogolemur* and either *Pseudotetonius ambiguus* (Bown, 1974; Krishtalka and Schwartz, 1978) or its close relative and possible descendant, *Tatmanius szalayii* (Bown and Rose, 1991). All of these taxa share derived features of the antemolar dentition, particularly the loss of  $P_2$  and the presence of a single-rooted  $P_3$  [here we follow the dental homologies proposed by Gazin (1958) and Bown and Rose

(1987) for *Trogolemur* and *Pseudotetonius*, respectively; these do not correspond with the dental homologies for these taxa identified by Bown (1974) and Krishtalka and Schwartz (1978)]. We remain unconvinced by arguments that link *Trogolemur* with derived anaptomorphinins such as *Pseudotetonius* and *Tatmanius* for several reasons: (1) the same modifications of the lower premolar dentition that typify *Trogolemur*, *Pseudotetonius* and *Tatmanius* have also occurred in other omomyids, particularly *Anemorhysis* (Bown and Rose, 1984); (2) the anagenetic nature of the transformation from the primitive lower premolar dentition of *Tetonius matthewi* to the more derived condition in *Pseudotetonius ambiguus* (Rose and Bown, 1984; Bown and Rose, 1987). This implies either that similarities in the lower premolar dentition shared by *Pseudotetonius* and *Trogolemur* are convergent or that *P. ambiguus* is directly ancestral to *Trogolemur*. However, *P. ambiguus* is unlikely to be directly ancestral to *Trogolemur* because *P. ambiguus* possesses derived dental features, including an hypertrophied, exodaenodont P<sub>4</sub> and greatly reduced upper and lower third molars that are lacking in *Trogolemur*. These same arguments mitigate against a possible relationship between *Trogolemur* and *Tatmanius*, which is plausibly a more derived descendant of *Pseudotetonius* (Bown and Rose, 1991); (3) as noted in the tribal diagnosis above, the upper and lower molars of *Trogolemur* are much more similar to those of other trogolemurinins than to those of anaptomorphinins such as *Tetonius*, *Pseudotetonius* and *Tatmanius*. The first upper molars of *Trogolemur* were reported recently by Emry (1990) from the Bridgerian Elderberry Canyon local fauna of Nevada and by Storer (1990) from the Lac Pelletier lower fauna of Saskatchewan (the upper molars of *Trogolemur* reported by Storer were attributed by him to *Phenacolemur leonardi*). These new specimens reveal that the upper molars of *Trogolemur* are very similar to those of *Tetonoides* (e.g., YPM-PU 17357; see Szalay, 1976: fig. 36) and *Arapahovius* (Savage and Waters, 1978; Bown and Rose, 1991). The upper molars of all of these taxa have strongly developed postprotocingula, and the lingual slopes of their protocones are reduced in comparison to those of Anaptomorphini (so that the apex of the protocone is situated near the lingual margin of the tooth). In addition, M<sup>3</sup> is very similar in these taxa in being larger than in most Anaptomorphini and in having a well-developed postprotocrista that is continuous with a crest that runs lingually from the metacone.

In summary, although the Wasatchian ancestry of *Trogolemur* is not entirely clear at present, it appears to lie broadly among the other genera included here in the Trogolemurini. A close relationship between *Trogolemur* and anaptomorphinins such as *Pseudotetonius* and *Tatmanius* is not supported by the available evidence.

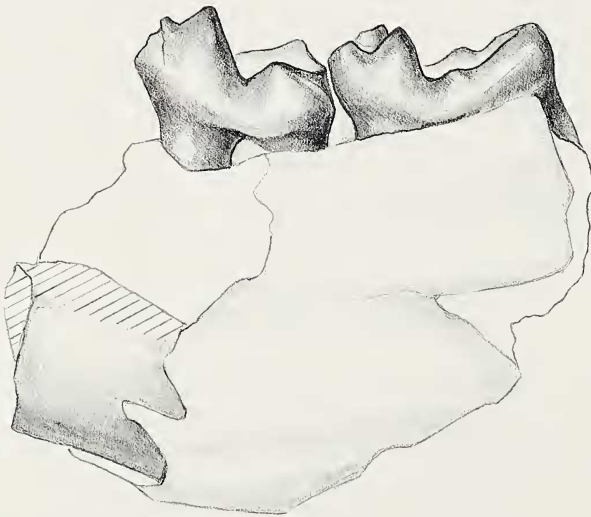
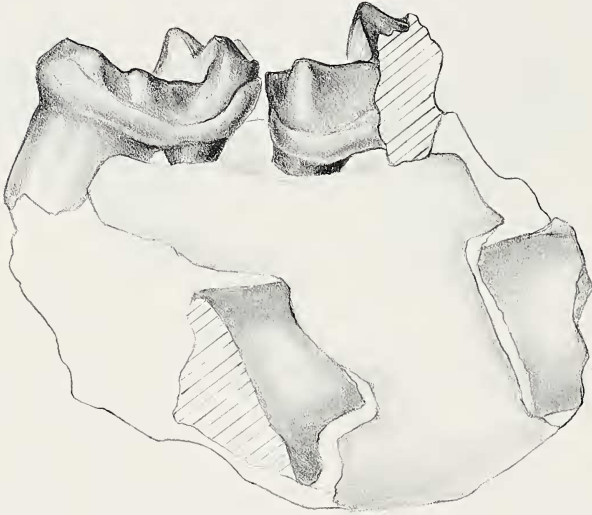
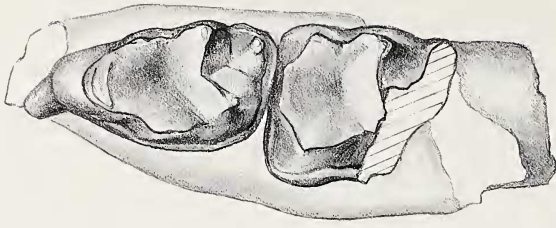
***Trogolemur fragilis*, new species**  
(Fig. 5)

*Holotype*.—CM 41152 (Fig. 5), right dentary fragment preserving M<sub>2</sub> (broken), M<sub>3</sub>, and distal part of root of I<sub>1</sub>.

*Hypodigm*.—The holotype and CM 40070, left dentary fragment preserving M<sub>3</sub> and distal part of root of I<sub>1</sub>.

*Type locality*.—CM loc. 34, Natrona County, Wyoming.

*Known distribution*.—*Eotitanops borealis* Assemblage Zone (Gardnerbuttean, earliest Bridgerian), Lost Cabin Member, Wind River Formation, Wind River Basin, Wyoming.



*Diagnosis.*—Much smaller than *T. amplior*, slightly smaller than *T. myodes*.  $M_3$  with paraconid less lingual in position, with distinct valley separating protoconid and metaconid, and with narrower talonid basin and hypoconulid lobe, all in contrast to *T. myodes*.

*Etymology.*—Latin *fragilis*, easily broken, brittle; in allusion to the fragmentary nature of the hypodigm.

*Description.*—The width of  $M_2$  in CM 41152 is 1.40 mm; the length of this tooth cannot be measured due to breakage of the mesial and buccal parts of the trigonid. In comparable aspects of anatomy,  $M_2$  in CM 41152 closely resembles this tooth in *T. amplior* (CM 40069).

$M_3$  measures 1.95 mm (L)  $\times$  1.20 mm (W) in both CM 41152 and CM 40070. Morphologically,  $M_3$  of *T. fragilis* differs from that of *T. myodes* in the features noted in the diagnosis.

Both known dentaries of *T. fragilis* show evidence of the enlarged root of  $I_1$  inferior to the molar roots. The distal part of the root of  $I_1$  is preserved in CM 41152, in which the structure is large and extends distally at least as far as the trigonid of  $M_3$ . In CM 40070 the alveolus for  $I_1$  is preserved at the level of the mesial break on the dentary (between  $M_2$  and  $M_3$ ); distal to this point the alveolus and/or root of  $I_1$  is obscured by matrix.

*Discussion.*—Although the species is very poorly known, *T. fragilis* can be assigned with confidence to *Trogolemur* because of the enlarged  $I_1$  extending distally through the dentary inferior to the roots of the lower molars. As noted previously, this condition occurs among omomyids only in the genus *Trogolemur*.

The hypodigm of *T. fragilis* was collected at CM loc. 34, a highly fossiliferous site that has yielded several thousand mammalian specimens (Stucky, 1984a). Hence, *T. fragilis* was apparently a very rare component of the fauna, and the potential for recovering significantly more complete specimens of the species in the near future is low.

Subfamily Omomyinae Trouessart, 1879

Tribe Washakiini Szalay, 1976

*Hemicodon* Marsh, 1872

*Hemicodon casamissus*, new species

(Fig. 6)

*Holotype.*—CM 62035 (Fig. 6), associated left and right dentary fragments preserving left  $M_2$ , talonid heel of left  $M_3$ , right  $M_{1-2}$ , and right  $P_3$  (right  $P_3$  not preserved in dentary fragment); only known specimen.

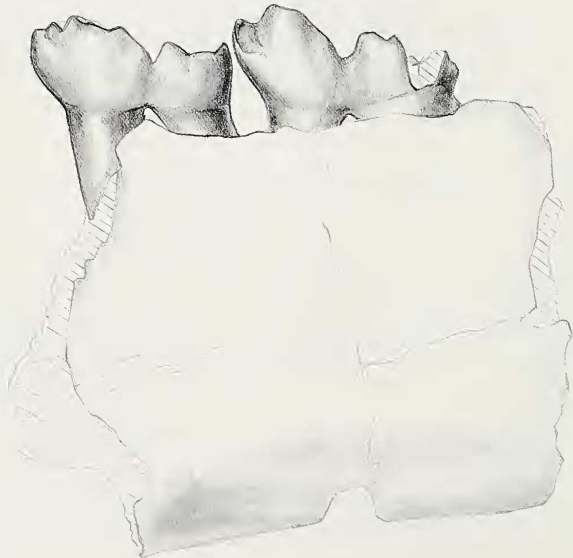
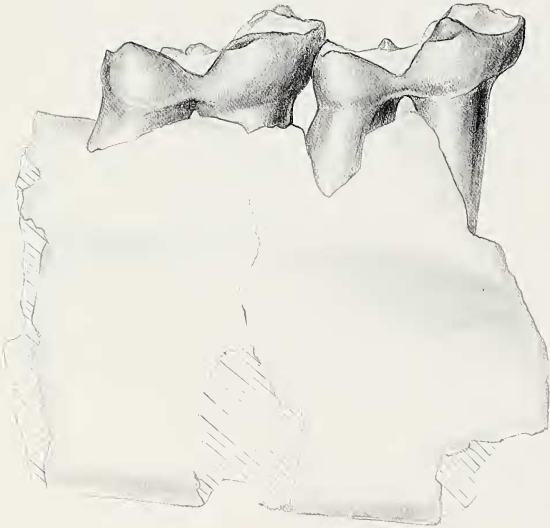
*Type locality.*—Level "A" (i.e., the lowest red mudstone and the underlying gray mudstones; see Stucky et al., 1990), CM loc. 1040, Natrona County, Wyoming.

*Known distribution.*—*Lambdotherium* Range Zone (Lostcabinian, latest Wasatchian), Lost Cabin Member, Wind River Formation, Wind River Basin, Wyoming.

*Diagnosis.*—Smaller than *H. gracilis*.  $P_3$  lower-crowned, without entoconid, with paracristid that curves slightly linguallly near its inferior end, and with narrower, more obliquely oriented postvallid lacking strong distolingual crest, all in contrast to *H. gracilis*.  $M_{1-2}$  with less crenulated enamel and with stronger talonid notch than in *H. gracilis*.

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Fig. 5.—*Trogolemur fragilis*, n. sp., holotype, CM 41152. Right dentary fragment preserving  $M_2$  (broken),  $M_3$  and distal part of root of  $I_1$ . Top to bottom: occlusal, buccal and lingual views. Scale equals 5 mm.



*Etymology.*—Latin *casa*, house, hut, cabin; and Latin *amissus*, lost; in allusion to the Lost Cabin Member of the Wind River Formation, provenance of the holotype.

*Description.*—The holotype and only known specimen of *H. casamissus* includes four associated fragments collected from a single small rill at CM loc. 1040 by Alan R. Tabrum in July 1989.

$P_3$  measures 2.75 mm (L)  $\times$  1.85 mm (W), and is double-rooted. The trigonid is simply constructed, being dominated by the protoconid and lacking both paraconid and metaconid. Mesially, the paracristid descends the apex of the protoconid before curving slightly lingually to become continuous with a mesiodistally short lingual cingulid. The latter structure does not extend distally to the level of the postvallid. The postvallid is obliquely oriented with respect to the long axis of the tooth, a distinction from the condition in *H. gracilis*, in which this structure is transverse in orientation. A weak crest descends the postvallid buccally. The talonid heel is mesiodistally short, labiolingually narrow, and simple in morphology, bearing only a buccally situated cuspule in the hypoconid position. A weak postcingulid runs lingually from this talonid cuspule before partly ascending the lingual aspect of the postvallid.

$M_1$  measures 2.90 mm (L)  $\times$  2.35 mm (W). The tooth is heavily worn, obscuring most details of crown morphology. However, it is clear that  $M_1$  in *H. casamissus* possessed the same distinctive proportions and occlusal outline typical of *H. gracilis*: the talonid is much wider in relation to the trigonid than in other omomyids due to the very buccal position of the hypoconid. Buccal to the  $M_1$  protoconid lies the remnant of a strong ectocingulid, as also occurs in *H. gracilis*. In contrast to the condition in the latter species, a well-developed talonid notch separates the entoconid from the postvallid in *H. casamissus*. Weakly incipient metastylid cuspules occur on the postvallids of  $M_{1-2}$  in CM 62035. The molar enamel is less crenulated in *H. casamissus* than is typical in *H. gracilis*. This is most evident on the relatively unworn lingual parts of the postvallids of  $M_{1-2}$  in CM 62035.

$M_2$  measures 3.20 mm (L)  $\times$  2.60 mm (W) (these measurements were taken from the slightly more complete right  $M_2$ ). Like that of  $M_1$ , the crown of  $M_2$  is heavily worn in CM 62035. Nevertheless, a few details of the crown morphology can be determined. In particular, the paraconid is situated farther buccally on  $M_2$  than on  $M_1$ , as is the case in *H. gracilis*. Otherwise,  $M_2$  is similar to  $M_1$  in showing the well-developed talonid notch, the weakly incipient metastylid (more apparent on the left  $M_2$  than on the right  $M_2$  in CM 62035), and the very wide talonid and strong ectocingulid characteristic of *Hemiacodon*.

$M_3$  is represented in CM 62035 only by a worn fragment of the left talonid, from which nothing of significance can be ascertained.

*Discussion.*—As noted by Gazin (1958, 1976) and Szalay (1976), all of the comparatively abundant fossils of *Hemiacodon gracilis* from the Bridger Basin of southwestern Wyoming for which stratigraphic provenance data are available were collected from rocks above the Sage Creek white layer (i.e., they come from the Twinbuttean = Bridger C and D; Krishtalka et al., 1987). Younger records of *Hemiacodon* have been reported by Lillegraven (1980) from the early Uintan Mission Valley Formation of San Diego County, California, and by Eaton (1985) from the early Uintan Wiggins Formation, Hot Springs County, Wyoming. *Hemiacodon casamissus* is therefore the geologically earliest record of the genus *Hemiacodon*, extending its known stratigraphic range from the late Bridgerian to the late Wasatchian.

There has been little consensus on the phylogenetic position of *Hemiacodon* with respect to other omomyids. Gazin (1958) made extensive comparisons between *Hemiacodon* and *Omomys*, regarding the former as an "omomyid" (essentially equivalent to the subfamily Omomyinae of many later authors; see Szalay, 1976). Gazin (1958) concluded that *Hemiacodon* was most closely related to *Utahia* and *Ourayia* among taxa known at that time.

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Fig. 6.—*Hemiacodon casamissus*, n. sp., holotype, CM 62035. Right dentary fragment preserving  $M_{1-2}$  and associated right  $P_3$ . Top to bottom: occlusal, buccal and lingual views. Scale equals 5 mm.

For a number of years, work on the Uintan primate fauna of the Uinta Basin of Utah supported Gazin's (1958) suggestion of a close relationship between *Hemiacodon* and *Ourayia*. For example, Simons (1961) described additional omomyid material from the Uinta Basin which led him to state that ". . . I suspect that the genus [*Ourayia*] may have been derived directly from *Hemiacodon* . . ." (Simons, 1961:5). Robinson (1968) later proposed the new species *Hemiacodon jepseni* on the basis of YPM-PU 16431, a specimen previously referred by Simons (1961) to *Ourayia uintensis*. Szalay (1976) synonymized *Hemiacodon jepseni* with *Ourayia uintensis*, but was the first person to argue against a close relationship between *Hemiacodon* and *Ourayia*. Krishtalka (1978) recognized the morphological distinctions between Robinson's (1968) "*Hemiacodon*" *jepseni* and *Ourayia uintensis*, and referred the former species to *Macrotarsius*, a classification that is supported here. Despite the confusing taxonomic history of Uinta Basin omomyid specimens (particularly YPM-PU 16431) that have been assigned to the genera *Ourayia*, *Hemiacodon*, and *Macrotarsius* by different workers, there is little support for a close relationship between *Hemiacodon* and either *Ourayia* or *Macrotarsius* at present.

There are three current hypotheses regarding the phylogenetic position of *Hemiacodon*. The first of these, and the one that we support, is that *Hemiacodon* is a uniquely specialized washakiin omomyid. Szalay (1976) noted many features that were shared between *Hemiacodon* and washakiins such as *Loveina*, and included the genus in his tribe Washakiini as a result. A similar conclusion was reached by Krishtalka and Schwartz (1978), who suggested that *Hemiacodon* is the sister group of a clade consisting of *Shoshonius*, *Washakius*, and *Dyseolemur* (see Krishtalka and Schwartz, 1978: fig. 6).

A second hypothesis, advanced by Honey (1990), holds that *Hemiacodon* shows merely convergent similarities to washakiin omomyids, and that it therefore bears no particularly close relationship to them. Rather, Honey (1990) suggested that *Hemiacodon* is the sister group to the tribe Omomyini. Honey's concept of Omomyini includes the genera *Omomys*, *Chumashius*, *Ourayia*, and *Macrotarsius*, but excludes *Steinius*, a genus that we would also classify as a primitive omomyinin. If valid, *Mytonius* can also be referred to the Omomyini.

A third possibility, which will not be evaluated here because we know of no morphological basis for it, is that *Hemiacodon* is the sister group of a clade consisting of the microchoerine genera *Necrolemur* and *Microchoerus* (Schwartz, 1986).

Honey's (1990) proposal that *Hemiacodon* may be the sister group of the Omomyini is based primarily on the omomyinin-like premolar construction found in *H. gracilis*. Specifically, he noted that  $P_{3-4}$  in *H. gracilis* are longer and narrower than in washakiins, and that, as in omomyinins, the protoconid of  $P_3$  is taller than that of  $P_4$  in *H. gracilis*.  $P_4$  is not yet known for *H. casamissus*, but the  $P_3$  of this species differs greatly from that of *H. gracilis* in ways that closely approximate the condition found in washakiins. In particular,  $P_3$  of *H. casamissus* is lower-crowned than that of *H. gracilis*, and it seems likely that it would not have been taller than  $P_4$ . Further, the trigonid of  $P_3$  in *H. casamissus* is mesiodistally shorter than that of *H. gracilis*, and it bears a paracristid that curves somewhat lingually near its inferior end, in contrast to the mesiodistally straight paracristid found in *H. gracilis*. In all of these aspects of  $P_3$  anatomy, *H. casamissus* closely resembles washakiins such as *Loveina* and *Washakius*. In sum, the anatomy of



$P_3$  in *H. casamissus* strongly suggests that this tooth in *H. gracilis* is autapomorphous and that the resemblances in lower premolar morphology between the latter species and omomyinins noted by Honey (1990) are convergent.

Honey (1990) also pointed out that  $I_1$  in *H. gracilis* is enlarged compared to  $I_2$  (see also Gazin, 1958; Szalay, 1976), as is the case in most omomyinins but contrary to the condition in washakiins. However,  $I_1$  is not enlarged in relation to  $I_2$  in the undoubted omomyinin *Chumashius balchi* (Szalay, 1976), and the anterior teeth of *Ourayia* remain unknown. Hypertrophy of  $I_1$  probably occurred independently in *H. gracilis* and in some omomyinins (Honey, 1990). Observations made by Gazin (1958:54) also support this view, as he noted that the difference in size between  $I_1$  and  $I_2$  is less in *H. gracilis* than in *Omomys*. Hence, the hypertrophy of  $I_1$  in *H. gracilis* is most likely autapomorphous. The relative size of these teeth is unknown in *H. casamissus*.

In contrast to the strong likelihood that the dental traits shared by *H. gracilis* and most omomyinins are the result of convergence, a number of features shared by *Hemicacodon* and certain washakiins appear to be valid synapomorphies, indicative of common ancestry. Honey (1990) has contributed the most exhaustive analysis of the evolution of the Washakiini achieved to date, and we accept almost all of his phylogenetic conclusions. In particular, Honey provided strong evidence that the evolution of well-developed metastylids and talonid notches on the lower molars occurred independently in the washakiin genus *Shoshonius* on the one hand and in a clade comprising the genera *Utahia*, *Stockia*, *Washakius*, and *Dyseolemur* on the other. *Hemicacodon casamissus* possesses strong talonid notches but only incipiently developed metastylids on its lower molars. These traits suggest that *H. casamissus* bears a close relationship with the *Utahia* + *Stockia* + *Washakius* + *Dyseolemur* clade, because in *Shoshonius* the development of strong metastylids apparently preceded the development of talonid notches on the lower molars (Honey, 1990). We suggest that the phylogenetic position of *Hemicacodon* lies nested within the former clade because a number of dental traits imply that *Hemicacodon* is the sister group of the clade comprising *Washakius* and *Dyseolemur*. These dental synapomorphies include: (1) strong, bulbous conules on  $M^{1-3}$ ; (2) incipient metastylids on  $M_{1-2}$ ; (3) paraconid of  $M_{2-3}$  more buccal in position than in other washakiins; (4) upper molar cusps (especially protocone) peripheral in position, yielding a relatively large trigon basin. In this context it should be emphasized that the upper dentition is not yet known in *H. casamissus*, and that the incipient metastylids observed on the known lower molars of *H. casamissus* are not found in *H. gracilis*. Nevertheless, the morphology of the upper molar dentition of *H. gracilis* and the morphology of the lower molar dentition of *H. casamissus* suggest that *Hemicacodon* is an aberrantly specialized washakiin, sharing its most recent common ancestry with the *Washakius* + *Dyseolemur* clade.

Tribe Uintaniini Szalay, 1976

*Uintanius* Matthew, 1915

*Uintanius rutherfordi* (Robinson, 1966), new combination  
(Fig. 7)

*Huerfanius rutherfordi*: Robinson, 1966:35.

*Uintanius ameghini*: Szalay, 1976:336; Szalay and Delson, 1979:248 (part).

*Uintanius rutherfordi*: Gingerich, 1981:358, incorrect subsequent spelling.

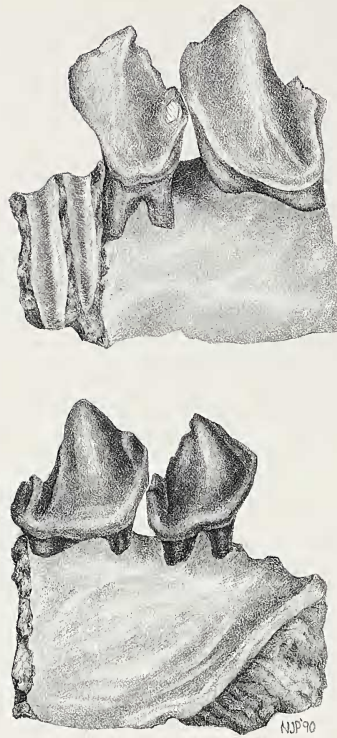


Fig. 7.—*Uintanius rutherfordi*, n. comb., UCM 44858. Left dentary fragment preserving alveoli for  $C_1$ - $P_2$  and crowns of  $P_{3-4}$ . Views are buccal (top) and lingual (bottom). Scale equals 10 mm.

*Referred material.*—UCM 44858, left dentary fragment preserving alveoli for  $C_1$ - $P_2$  and crowns of  $P_{3-4}$  (Fig. 7).

*Locality.*—UCM loc. 80061; *Eotitanops borealis* Assemblage Zone (Gardnerbuttean, earliest Bridgerian), Lost Cabin Member, Wind River Formation, Wind River Basin, Wyoming.

*Discussion.*—UCM 44858 provides both the oldest known record of *Uintanius* in Wyoming and the first record of the species *U. rutherfordi* in the state. It demonstrates that uintaniinins had appeared in Wyoming by at least Gardnerbuttean time, contrary to the statement by Beard (1987:465) that “Uintaniinins do not appear in the extensively documented Eocene fossil record of Wyoming until well into Bridgerian time. . . .” Otherwise, *U. rutherfordi* is known only from rocks of roughly equivalent age in the Huerfano Formation of southern Colorado (Robinson, 1966).

*Uintanius rutherfordi* was originally classified as a distinct genus, “*Huerfanius*,” on the basis of purported differences in the premolar dentition (Robinson, 1966). In his diagnosis of “*Huerfanius*,” Robinson (1966) cited the *Absarokius*-like mor-

phology of the lower premolars as the major distinction between “*Huerfanius*” and *Uintanius*. Expanded samples of both *U. ameghini* and *U. rutherfordi* recovered since 1966 reveal that the differences in premolar morphology between these two species are very minor, warranting specific rather than generic separation (also see Szalay, 1976). However, Szalay’s (1976) suggestion that these differences are actually the result of comparing deciduous and permanent premolars of the same species can no longer be sustained (Bown and Rose, 1984). The paraconid of P<sub>4</sub> in *U. rutherfordi* is weaker and slightly more inferior and lingual in position than that in *U. ameghini*. In the latter species the paraconid forms a pillar-like structure that is situated directly mesial to the protoconid, and very near the apex of that cusp. UCM 44858 is indistinguishable from the known specimens of *U. rutherfordi* (i.e., AMNH 55216, UCM 26533) from the Huerfano Formation in these aspects of lower premolar morphology.

#### DISCUSSION

The phylogenetic implications of the new omomyid species described in this paper have already been assessed. Here, we discuss the possible significance of this new material for understanding the distinct taxonomic reorganization of the omomyid primate fauna that took place across the Wasatchian-Bridgerian boundary in North America. Our discussion focuses on the Wasatchian and Bridgerian record of omomyid evolution in Wyoming, for two main reasons: (1) the fossil record for this time interval is generally more complete in Wyoming than elsewhere in North America, although important, partly contemporaneous mammalian assemblages containing omomyids also occur in other western states (i.e., Colorado, Utah, Nevada, and New Mexico; see Gazin, 1958; Robinson, 1966; Szalay, 1976; Beard, 1987; Honey, 1990; Emry, 1990); (2) to minimize confounding factors related to paleobiogeography, it is necessary to concentrate on the pattern of temporal change in omomyid taxonomic composition in a limited geographic area.

In general, Wasatchian omomyid faunas of western North America are dominated by anaptomorphines, while omomyines form the major component of omomyid faunas of Bridgerian and younger age (e.g., Szalay, 1976; Bown, 1979*b*). With one exception, this generalization holds with respect to both individual abundance and species richness in Wyoming. This exception is the Bridgerian omomyid fauna from the Aycross Formation in the northwestern part of the state (Bown, 1979*b*, 1982; Honey, 1990), which is numerically dominated by anaptomorphines (there is no consensus at present regarding the number of valid anaptomorphine species represented in the Aycross sample; see Bown, 1979*b*, 1982; Gingerich, 1981; Szalay, 1982; Bown and Rose, 1987). This interesting exception will be discussed further below.

The stratigraphic distributions of omomyid genera known from middle Wasatchian (Lysitean) through Bridgerian rocks in Wyoming are provided in Table 1; biostratigraphic subdivisions follow Krishtalka et al. (1987). The data support the generalizations noted above concerning omomyid taxonomic composition through time: the only anaptomorphines known from post-Wasatchian rocks are *Absarokius* and *Anemorhysis* (which apparently become extinct during Gardnerbuttean or earliest Bridgerian time), the rare genera *Anaptomorphus* and *Trogolemur*, and Aycross taxa *Strigorhysis*, *Aycrossia*, and *Gazinius*. According to Gingerich (1981) and Szalay (1982), who variously synonymized the Aycross genera *Strigorhysis*, *Aycrossia*, and *Gazinius* with *Absarokius* and *Anaptomorphus*, even

this relatively low diversity of post-Wasatchian anaptomorphines is exaggerated. Conversely, the only omomyines known from Wasatchian rocks in Wyoming are the primitive omomyinin *Steinius* (known from late Graybullian and Lysitean rocks of the Bighorn Basin; Bown and Rose, 1984, 1987, 1991; Rose and Bown, 1991), the primitive washakiin *Loveina* (known from Lysitean and Lostcabinian rocks of the Wind River Basin and elsewhere; Bown and Rose, 1984; Stucky, 1984c), and the more derived washakiins *Shoshonius* and *Hemiacodon* (both of which first appear in Lostcabinian rocks of the Wind River Basin).

The upper part of the Wind River Formation provides a nearly continuous record of mammalian evolution across the Wasatchian-Bridgerian boundary (Stucky 1984a, 1984b, 1984c; Krishtalka et al., 1987). It therefore comes as no great surprise that the Wind River record reveals that the change in omomyid taxonomic composition across this boundary was more gradual than it would otherwise appear. In particular, the Wind River record reveals that omomyines were more diverse in Wyoming during the middle and late Wasatchian and the earliest Bridgerian than the record from elsewhere in the state would suggest (Table 1). For example, *Loveina* is known from both Lysitean and Lostcabinian rocks in the Wind River Basin, but only from Lostcabinian rocks elsewhere in Wyoming. *Shoshonius* and *Hemiacodon* are both represented in Lostcabinian rocks of the

Table 1.—Stratigraphic distributions of omomyid genera known from middle Wasatchian through Bridgerian rocks in Wyoming. Abbreviations: LY, Lysitean; LO, Lostcabinian; GA, Gardnerbuttean; BL, Blackforkian; TW, Twinbuttean. Letters represent the following sources, on which this compilation is based: (A) Szalay, 1976; (B) Gazin, 1976; (C) Savage and Waters, 1978; (D) Bown, 1979b; (E) Stucky, 1984a; (F) Stucky, 1984c; (G) Bown and Rose, 1984; (H) Bown and Rose, 1987; (I) Honey, 1990; (J) this paper. References are not meant to be exhaustive.

	LY	LO	GA	BL	TW
Anaptomorphinae					
Anaptomorphini					
<i>Absarokius</i>	A	A	E	—	—
<i>Chlororhysis</i>	—	A	—	—	—
<i>Anaptomorphus</i>	—	—	F	B	—
<i>Strigorhysis</i>	—	H	—	D	—
<i>Aycrossia</i>	—	—	E	D	—
<i>Gazinius</i>	—	—	—	D	—
Trogolemurini					
<i>Anemorhysis</i>	G	A	J	—	—
<i>Trogolemur</i>	—	—	J	B	—
<i>Arapahovius</i>	C	—	—	—	—
Omomyinae					
Uintaniini					
<i>Uintanius</i>	—	—	J	B	A
Omomyini					
<i>Steinius</i>	G	—	—	—	—
<i>Omomys</i>	—	—	F	B	B
Washakiini					
<i>Hemiacodon</i>	—	J	—	—	B
<i>Washakius</i>	—	—	E	B	B
<i>Loveina</i>	G	E	—	—	—
<i>Shoshonius</i>	—	E	E	I	—

Wind River Formation, but are restricted to Blackforkian and Twinbuttean rocks, respectively, elsewhere in the state. *Washakius* and *Uintanius* first appear in the Wind River Basin during Gardnerbuttean time, but these genera are restricted to later Bridgerian rocks elsewhere in Wyoming. The highly derived anaptomorphine *Trogolemur*, otherwise restricted to Blackforkian and Twinbuttean time, also first appears during the Gardnerbuttean in the Wind River Basin. In addition to these earlier records of omomyid genera otherwise known only from later in Bridgerian time in Wyoming, there is evidence in the Wind River Formation of the persistence into the earliest Bridgerian of *Anemorhysis*, a genus otherwise restricted to the Wasatchian.

In summary, the later Wasatchian and earliest Bridgerian fossil record of the Wind River Basin seems to document a gradual shift in taxonomic composition from omomyid faunas of "Wasatchian aspect" (dominated by anaptomorphines) to omomyid faunas of "Bridgerian aspect" (dominated by omomyines). The Gardnerbuttean appears to have been an especially pivotal interval for turnover in omomyid faunal composition, as it was distinguished by the coexistence of typically Wasatchian taxa, such as *Anemorhysis* and *Absarokius*, and common Bridgerian forms, such as *Washakius*, *Uintanius*, and *Trogolemur*. Other components of the Gardnerbuttean mammalian fauna also show this coexistence of characteristically Wasatchian and Bridgerian forms (Stucky, 1984c). The Wasatchian-Bridgerian faunal turnover had a considerable impact on the later evolution of omomyids in North America, as anaptomorphines are essentially unknown from post-Bridgerian faunas on the continent, while omomyines continued to diversify there. Only the rare and dentally specialized anaptomorphine genus *Trogolemur* appears to have survived in North America beyond Bridgerian time (Robinson, 1968; Szalay, 1976; Krishtalka, 1978; Storer, 1990).

What factors could have caused the taxonomic restructuring of the omomyid primate fauna that took place across the Wasatchian-Bridgerian boundary in Wyoming? The available data do not provide a definitive answer to this question, but one factor, climatic warming, may be cited as a potential candidate. The late Wasatchian and early Bridgerian were characterized by the warmest climatic conditions known for the entire Cenozoic (Savin, 1977; Wolfe, 1978, 1986). It would not be surprising if this peak in tropicality affected the geographic distributions of plant and animal taxa. For example, Wing (1987:754) noted that "During the Wasatchian and Bridgerian there appears to have been a major poleward expansion of subtropical and paratropical forest types in response to [this] global climatic warming. . . ." Likewise, Beard (1987, 1988) suggested that several mammalian clades, including the primate taxa *Smilodectes* and *Uintaniini*, may have expanded their ranges poleward during this interval in association with the contemporaneous climatic and floral changes. Similarly, climatic warming may have contributed to the gradual replacement of a more northern omomyid fauna (dominated by anaptomorphines) by a more southern omomyid fauna (dominated by omomyines) beginning in the Lostcabinian.

This hypothesis has already been suggested in the case of the omomyine tribe *Uintaniini*, which first appears in rocks of late Graybullian or Lysitean age in the San Jose Formation, San Juan Basin, New Mexico, well before its first appearance in Wyoming during Gardnerbuttean time (Beard, 1987; also see above). The only other omomyid currently known from the San Jose Formation was listed as an indeterminate genus and species by Beard (1987), although the likelihood that it actually represented a second omomyine species was recognized at that time

(Beard, 1987:464). Further examination and comparisons of the most complete of these specimens (UALP 11231; see Beard, 1987: fig. 2f) suggest that it probably represents the washakiin genus *Loveina*, and it is here referred to *Loveina* sp., cf. *L. minuta*. If this allocation is correct, UALP 11231 represents one of the earliest occurrences of the omomyine tribe Washakiini (along with the holotype and only known specimen of *Loveina minuta*, ACM 3365, from the Lysite Member of the Wind River Formation). Anaptomorphines have yet to be reported from the San Jose Formation. Thus, the available (though meager) evidence suggests that the San Jose omomyid fauna was dominated by omomyines at a time (middle Wasatchian) when omomyid faunas in Wyoming were dominated by anaptomorphines. A much richer omomyid record from the San Jose Formation and other southern rock units is required to test this hypothesis.

Further evidence that offers circumstantial support for a climatic role in the restructuring of omomyid taxonomic composition across the Wasatchian-Bridgerian boundary comes from the Bridgerian omomyid fauna of the Aycross Formation, Absaroka Range, northwestern Wyoming (Bown, 1979*b*, 1982; Honey, 1990). The omomyids here are predominantly anaptomorphines. As many as four genera and five species of anaptomorphines are known from the Aycross Formation (Bown, 1979*b*, 1982), while only two omomyine species are currently recorded from these rocks (Bown, 1982; Honey, 1990). Thus, the omomyid fauna from the Aycross Formation is unusual in exactly the opposite way that the omomyid fauna from the San Jose Formation appears to be: it was dominated by anaptomorphines at a time (Blacksforkian) when other known omomyid faunas were dominated by omomyines. All of the latter faunas are derived from rocks that were deposited in early Tertiary basins, and they may therefore represent a more lowland community than does the Aycross fauna, which is derived from volcanoclastic rocks of the Absaroka volcanic province (Bown, 1979*b*, 1982; Black, 1967).

The otherwise anomalous omomyid faunas from the San Jose and Aycross formations are both consistent with the hypothesis that climatic warming contributed to the turnover in omomyid faunal composition across the Wasatchian-Bridgerian boundary in Wyoming. Under this hypothesis, the omomyids known from the San Jose Formation can be viewed as being representative of the omomyid fauna of the southern part of western North America during Wasatchian time. This poorly sampled southern Wasatchian omomyid fauna was dominated by omomyines at the same time that the much better sampled northern omomyid fauna was dominated by anaptomorphines. Poleward expansion of the range of the more southerly, omomyine-dominated fauna, associated with global climatic warming and poleward range expansion of certain plant taxa during the late Wasatchian and early Bridgerian, would therefore have resulted in the Wasatchian-Bridgerian turnover in omomyid faunal composition that is observed in the northern part of the western United States (i.e., Wyoming). Conversely, the anaptomorphine-dominated omomyid fauna of the Aycross Formation may reflect the existence, during early Bridgerian time, of an upland refugium for the more northerly, anaptomorphine-dominated fauna, which by this time had largely been replaced in the intermontane basins of Wyoming (Bown, 1979*b*; Black, 1967). Judging from the overwhelming predominance of omomyines in post-Bridgerian faunas throughout North America, the Anaptomorphinae never recovered from the restructuring of the omomyid fauna that took place across the Wasatchian-Bridgerian boundary, regardless of what its ultimate causes may have been.

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## LITERATURE CITED

- BEARD, K. C. 1987. *Jemezius*, a new omomyid primate from the early Eocene of northwestern New Mexico. *Journal of Human Evolution*, 16:457–468.
- . 1988. New notharctine primate fossils from the early Eocene of New Mexico and southern Wyoming and the phylogeny of Notharctinae. *American Journal of Physical Anthropology*, 75: 439–469.
- BLACK, C. C. 1967. Middle and late Eocene mammal communities: a major discrepancy. *Science*, 156:62–64.
- BOWN, T. M. 1974. Notes on some early Eocene anaptomorphine primates. *University of Wyoming, Contributions to Geology*, 13:19–26.
- . 1979a. Geology and mammalian paleontology of the Sand Creek facies, lower Willwood Formation (lower Eocene), Washakie County, Wyoming. *Geological Survey of Wyoming Memoir*, 2:1–151.
- . 1979b. New omomyid primates (Haplorhini, Tarsiiformes) from middle Eocene rocks of west-central Hot Springs County, Wyoming. *Folia Primatologica*, 31:48–73.
- . 1982. Geology, paleontology, and correlation of Eocene volcanoclastic rocks, southeast Absaroka Range, Hot Springs County, Wyoming. *U.S. Geological Survey Professional Paper*, 1201A: 1–75.
- BOWN, T. M., AND K. D. ROSE. 1984. Reassessment of some early Eocene Omomyidae, with description of a new genus and three new species. *Folia Primatologica*, 43:97–112.
- . 1987. Patterns of dental evolution in early Eocene anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. *Paleontological Society Memoir*, 23:1–162.
- . 1991. Evolutionary relationships of a new genus and three new species of omomyid primates (Willwood Formation, lower Eocene, Bighorn Basin, Wyoming). *Journal of Human Evolution*, 20:465–480.
- COPE, E. D. 1881. On the Vertebrata of the Wind River Eocene beds of Wyoming. *U.S. Geological and Geographic Surveys of the Territories, Bulletin*, 6:183–202.
- EATON, J. G. 1985. Paleontology and correlation of the Eocene Tepee Trail and Wiggins formations in the North Fork of Owl Creek area, southeastern Absaroka Range, Hot Springs County, Wyoming. *Journal of Vertebrate Paleontology*, 5:345–370.
- EMRY, R. J. 1990. Mammals of the Bridgerian (middle Eocene) Elderberry Canyon local fauna of eastern Nevada. *Geological Society of America Special Paper*, 243:187–210.
- GAZIN, C. L. 1952. The lower Eocene Knight Formation of western Wyoming and its mammalian faunas. *Smithsonian Miscellaneous Collections*, 117:1–82.
- . 1958. A review of the middle and upper Eocene primates of North America. *Smithsonian Miscellaneous Collections*, 136:1–112.
- . 1962. A further study of the lower Eocene mammalian faunas of southwestern Wyoming. *Smithsonian Miscellaneous Collections*, 144:1–98.
- . 1976. Mammalian faunal zones of the Bridger middle Eocene. *Smithsonian Contributions to Paleobiology*, 26:1–25.
- GEBO, D. L. 1988. Foot morphology and locomotor adaptation in Eocene primates. *Folia Primatologica*, 50:3–41.
- GINGERICH, P. D. 1981. Early Cenozoic Omomyidae and the evolutionary history of tarsiiform primates. *Journal of Human Evolution*, 10:345–374.
- HONEY, J. G. 1990. New washakiin primates (Omomyidae) from the Eocene of Wyoming and Colorado, and comments on the evolution of the Washakiini. *Journal of Vertebrate Paleontology*, 10:206–221.
- KRISHTALKA, L. 1978. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 15. Review of the late Eocene primates from Wyoming and Utah, and the Plesitarsiiformes. *Annals of Carnegie Museum*, 47:335–360.

- KRISHTALKA, L., AND J. H. SCHWARTZ. 1978. Phylogenetic relationships of plesiadapiform-tarsiiform primates. *Annals of Carnegie Museum*, 47:515-540.
- KRISHTALKA, L., R. K. STUCKY, R. M. WEST, M. C. MCKENNA, C. C. BLACK, T. M. BOWN, M. R. DAWSON, D. J. GOLZ, J. J. FLYNN, J. A. LILLEGRAVEN, AND W. D. TURNBULL. 1987. Eocene (Wasatchian through Duchesnean) biochronology of North America. Pp. 77-117, in *Cenozoic Mammals of North America: Geochronology and Biostratigraphy* (M. O. Woodburne, ed.), University of California Press, Berkeley, xv + 336 pp.
- LILLEGRAVEN, J. A. 1980. Primates from later Eocene rocks of southern California. *Journal of Mammalogy*, 61:181-204.
- MATTHEW, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. *Memoirs of the American Museum of Natural History*, 9:289-567.
- ROBINSON, P. 1966. Fossil Mammalia of the Huerfano Formation, Eocene, of Colorado. *Yale University, Peabody Museum of Natural History, Bulletin*, 21:1-95.
- . 1968. The paleontology and geology of the Badwater Creek area, central Wyoming. Part 4. Late Eocene primates from Badwater, Wyoming, with a discussion of material from Utah. *Annals of Carnegie Museum*, 39:307-326.
- ROSE, K. D., AND T. M. BOWN. 1984. Gradual phyletic evolution at the generic level in early Eocene omomyid primates. *Nature*, 309:250-252.
- . 1991. Additional fossil evidence on the differentiation of the earliest euprimates. *Proceedings of the National Academy of Sciences*, 88:98-101.
- SAVAGE, D. E., AND B. T. WATERS. 1978. A new omomyid primate from the Wasatch Formation of southern Wyoming. *Folia Primatologica*, 30:1-29.
- SAVIN, S. M. 1977. The history of the Earth's surface temperature during the past 100 million years. *Annual Review of Earth and Planetary Sciences*, 5:319-355.
- SCHWARTZ, J. H. 1986. Primate systematics and a classification of the order. Pp. 1-41, in *Comparative Primate Biology, Volume 1: Systematics, Evolution, and Anatomy* (D. R. Swindler and J. Erwin, eds.), Alan R. Liss, New York, 816 pp.
- SIMONS, E. L. 1961. The dentition of *Ourayia*: its bearing on relationships of omomyid prosimians. *Yale University, Postilla*, 54:1-20.
- STORER, J. E. 1990. Primates of the Lac Pelletier lower fauna (Eocene: Duchesnean), Saskatchewan. *Canadian Journal of Earth Sciences*, 27:520-524.
- STUCKY, R. K. 1982. Mammalian fauna and biostratigraphy of the upper part of the Wind River Formation (early to middle Eocene), Natrona County, Wyoming, and the Wasatchian-Bridgerian boundary. Unpublished Ph.D. dissert., University of Colorado, Boulder, 278 pp.
- . 1984a. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 5. Geology and biostratigraphy of the upper part of the Wind River Formation, northeastern Wind River Basin. *Annals of Carnegie Museum*, 53:231-294.
- . 1984b. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 6. Stratigraphic sections and locality descriptions, upper part of the Wind River Formation. *Annals of Carnegie Museum*, 53:295-325.
- . 1984c. The Wasatchian-Bridgerian Land Mammal Age boundary (early to middle Eocene) in western North America. *Annals of Carnegie Museum*, 53:347-382.
- STUCKY, R. K., L. KRISHTALKA, AND A. D. REDLINE. 1990. Geology, vertebrate fauna, and paleoecology of the Buck Spring Quarries (early Eocene, Wind River Formation), Wyoming. *Geological Society of America Special Paper*, 243:169-186.
- SZALAY, F. S. 1976. Systematics of the Omomyidae (Tarsiiformes, Primates): taxonomy, phylogeny, and adaptations. *Bulletin of the American Museum of Natural History*, 156:157-450.
- . 1982. A critique of some recently proposed Paleogene primate taxa and suggested relationships. *Folia Primatologica* 37:153-162.
- SZALAY, F. S., AND E. DELSON. 1979. *Evolutionary History of the Primates*. Academic Press, New York, 580 pp.
- WING, S. L. 1987. Eocene and Oligocene floras and vegetation of the Rocky Mountains. *Annals of the Missouri Botanical Gardens*, 74:748-784.
- WOLFE, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist*, 66:694-703.
- . 1986. Tertiary floras and paleoclimates of the Northern Hemisphere. University of Tennessee Department of Geological Sciences, *Studies in Geology*, 15:182-196.